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THE OCCURRENCE AND INHERITANCE OF SEX INTERGRADATION IN PLANTS

CECIL YAMPOLSKY

In a previous paper (1919) I have called attention to sex intergradation in *Mercurialis annua* in both male and female cultures. It is my purpose here to discuss the general question of sex intergrades as they occur in the flowering plants. This discussion is based in a large measure upon the results reported in the paper mentioned above.

There can be no question from the data at hand that sex in *Mercurialis* is a fluctuating rather than a fixed character expressing itself in a wide range of sex intergrades, including as the extremes some pure male and some pure female plants and midway between the extremes highly fertile monoecious forms. The sex intergrades here are all highly and equally fertile, and no suspicion of abnormality or of pathological conditions can attach to them. That there is a tendency to pure dioecism seems highly probable, but the transition from hermaphroditism is still represented by all possible gradations, showing most convincingly that theories of sex determination based on the segregation of fixed unit factors can have no significance for such types.

SEX INTERGRADES

Goldschmidt (1916a) reports in a preliminary paper upon the sex ratios in crosses between the European and Japanese races of the gypsy moth, *Lymantria dispar*. He obtains various gradations in the sexual condition unlike the well known gynandromorphs. His individuals do not, as in the case of the gynandromorphs, show a sectorial arrangement of the characters of the two sexes, but they do show different gradations between the extremes of femaleness and maleness. His females show all the transition stages, such as feathered antennae, male wing pigmentation, the transition of ovaries into testes, and the loss of the power to lay eggs. His males show tendencies towards femaleness in a similar manner. For these individuals he proposes the term *intersexes*. He finds that as his sex intergrades approach the middle line between maleness and femaleness, they become more and more sterile, that is he obtains no fertile hermaphrodites such as occur for example in *Mercurialis annua*. In fact, although his forms show morphological intersexualism, they are functionally sexless in many instances. To be sure, he secures his intergrades by using as parents forms which in themselves possess functional sexual intergradation. As noted in my previous paper, there is a tendency in plant forms that exhibit gradations in sex (judged by the proportion of male, female, and hermaphro-

ditic flowers) to show a definite influence of that condition upon the sex ratios in the offspring.

Banta (1916) reports the appearance of intersexes in a phyllopod, *Limocephalus vetulus*. The females reproduce parthenogenetically. "In one of the strains there appeared a large percentage of males together with normal females and a large number of sex intergrades—males with one or more female secondary sex characters, females with one to several male characters, and some hermaphrodites with various combinations of male and female secondary sex characters." Eight secondary sex characters distinguish the male from the female. The highly male-like female intergrades are relatively infertile. The more the female takes on the male characters the less likely she is to be fertile. Some individuals with several secondary male characters prove to be very fertile. "In general in addition to being more prolific one may say that female intergrades with few or less distinctly male characters produce a smaller percentage of males and sex intergrades than those having a larger number of more definitely male characters." Males that show one or more female secondary sex characters nearly always have an incompletely developed reproductive system. By propagating from female intergrades, Banta was able to secure the production of mixed broods, males, females, and sex intergrades. The stock derived from these females consists of 40 percent normal males, 8 percent normal females, and the rest intergrades with almost any combination of male and female secondary and primary sex characters. Some of his sex intergrades (female) may parthenogenetically produce normal females and occasionally normal males.

In a later paper, Banta (1918) reports on sex intergrades in *Daphnia longispina*. In this form the male differs from the female in eight secondary sex characters. In *Daphnia* there are fewer male than female intergrades. The offspring of the more highly male female intergrades tend to be like the mother. A female from a sex intergrade will produce offspring very much like herself with few male secondary sex characters. The more male the female intergrade, the more sterile she is likely to be.

Banta makes the following suggestive remark: "From such clear cases of sex intermediates one wonders if maleness and femaleness are really mutually exclusive in those Cladocera individuals which morphologically show no unlike sex characters. Even in 'normal' strains one is certainly justified in thinking that maleness and femaleness are not complete and mutually exclusive states but that in these apparently normal sex forms, too, sex is also relative—differing from so-called sex intergrades not in kind but merely in degree, not qualitatively but quantitatively."

Plants show most clearly that maleness and femaleness in the same individual do not tend to neutralize each other and to produce sterility. The appearance of intersexes or sex intergrades in the plant kingdom, while not designated by these terms, has been described for very many forms in the

phanerogamic floras. A definite terminology is used in botanical literature to cover this phenomenon. The terms *hermaphroditic*, *dioecious*, *monoecious*, *andromonoecious*, *gynomonoecious*, *trimonoecious*, *gynodioecious*, *trioecious*, *androdioecious*, etc., are used.

A hermaphroditic form is one in which both pistils and stamens are borne in the same flower (perfect flower), and in which all the flowers on a plant show the same arrangement of parts. Example: *Lilium*.

A dioecious form is one in which the sexes are completely separated so that one plant bears male flowers only and the other plant female flowers only. Example: *Elodea canadensis*.

A monoecious form is one in which the pistillate and staminate inflorescences are borne separately on the same plant. Example: *Begonia*.

An andromonoecious form is one that bears perfect flowers and male flowers on the same plant. Example: many Umbelliferae (Lotsy, 1911).

A gynomonoecious form is one that bears perfect flowers and female flowers on the same plant. Example: *Atriplex* and many Compositae (Lotsy, 1911).

A trimonoecious form is one that has three distinct types of flowers, male, female, and hermaphroditic. Example: *Acer campestre* (Lotsy, 1911).

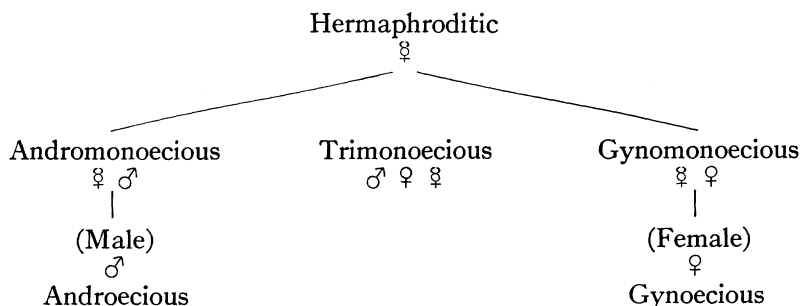
A gynodioecious form is one that has both female and hermaphroditic individuals. Example: *Plantago lanceolata*.

An androdioecious form is one that has both male and hermaphroditic individuals. Example: *Caltha palustris* (Lotsy, 1911).

Other combinations may occur. Staminate and pistillate inflorescences may appear on one individual and hermaphroditic on another. Example: *Callitriche* (Lotsy, 1911). Male and female inflorescences may appear on one individual while another individual may be male. Example: *Ceretopus* (Lotsy, 1911). Male and female inflorescences may appear on one individual while another may have only female flowers. Example: *Morus* (Lotsy, 1911). Hermaphroditic and male flowers may appear on one individual while another is female only. Example: *Gleditsia* (Lotsy, 1911).

A trioecious form is one in which three distinct sex types occur, male, female, and hermaphroditic. Example: hemp.

Correns (1913) offers the following diagram to show these conditions.



He proposes to call these forms *mixed in sex*. The old term is *polygamous*. I have used the term *intersexes* or *sex intergrades*.

These groups indicate in every case the distribution of functional sex elements. We find, however, just as Goldschmidt found in his intersexes, so here, that every possible degree of functional and structural perfection and degeneration exists and has been long known, though botanists have been inclined to take them as matters of course until the development of the recent efforts to make sex determination a matter of absolutely alternative inheritance and to represent sex characters by fixed and invariable factors in the germ plasm which are segregated in the reduction division. We can classify the grades of development of female sex organs as follows. In each case functional stamens are present in the same flower or elsewhere on the same plant.

I. Functional Variation.

- a. Ovaries fertile to pollen from another genus: *Zea Mays* L. \times *Euchlaena Mexicana* Schrad.
- b. Ovaries fertile to pollen from one or more different species: *Antirrhinum molle* \times *A. majus*.
- c. Ovaries both cross- and self-fertile: *Zea Mays*.
- d. Ovaries cross-fertile and self-fertile: *Pyrus malus*.
- e. Ovaries normal in appearance but both cross- and self-sterile: *Eschscholtzia*.

II. Structural Variation.

- a. Ovaries normal in size, all ovules functional: *Lilium canadense*.
- b. Ovaries normal in size, ovules more or less aborted: *Phaseolus*.
- c. Ovaries normal in size, all ovules aborted: *Trifolium pratense*, *Syringa* hybrids.
- d. Ovaries visibly degenerate: *Fraxinus excelsior*.
- e. Ovaries mere rudiments: *Fraxinus excelsior*.
- f. Ovaries becoming stamen-like: *Salix caprea*.
- g. Ovaries not present, replaced by petals: *Matthiola*.

In the same way we can classify the grades of development of the male sex organs. In each case functional ovaries are present in the same flower or elsewhere on the same plant.

I. Functional Variation.

- a. Pollen capable of fertilizing ovaries of another genus: *Zea Mays* \times *Euchlaena Mexicana* Schrad.
- b. Pollen capable of fertilizing ovaries of another species: *Antirrhinum molle* \times *A. majus*.
- c. Pollen both cross- and self-fertile: *Zea Mays*.
- d. Pollen cross-fertile and self-sterile: *Pyrus malus*.
- e. Pollen normal in appearance but both cross- and self-sterile: *Eschscholtzia*.

II. Structural Variation.

- a. Anthers normal in size, all grains functional: *Lilium canadense*.
- b. Anthers normal in size, not all pollen grains functional: *Phaseolus*.
- c. Anthers normal in size, some pollen grains aborted: *Oenothera* hybrids.
- d. Anthers visibly degenerate: *Thymus vulgaris*.
- e. Anthers mere rudiments: *Echium vulgare*.
- f. Anthers becoming pistil-like: *Salix caprea*.
- g. Anthers not present, replaced by petals: *Matthiola*.

Further, as the classification shows, a great many plants exhibit gradations between maleness and femaleness and hermaphroditism because of the more or less nearly complete degeneration or modification of parts. A female may arise from a hermaphrodite through the more or less complete suppression or degeneration of stamens. Likewise a monoecious individual may become female by the degeneration or the entire suppression of the stamens. A male may arise from either one of such forms by the disappearance or more or less nearly complete degeneration of the carpels. When in a group of hermaphrodites the stamens of some of the plants are suppressed or degenerated we have a condition of gynodioecism, if the carpels are suppressed or degenerate a condition of androdioecism. When only parts of the plants exhibit the phenomena described we find a multiplicity of combinations. A gynomonoecious individual may arise from a hermaphrodite in which female flowers appear through the suppression or degeneration of the stamens. An andromonoecious individual may arise from a hermaphrodite through the suppression or degeneration of some of the carpels. Gynomonoecism and andromonoecism, just as well as gynodioecism and androdioecism, may appear in various gradations; in the former instance by virtue of the suppression or degeneration of larger or smaller numbers of parts of the plant, and in the latter case because of changes that may occur in larger or smaller numbers of individuals in a group of plants.

The appearance of sporadic female or male flowers on a hermaphroditic plant may bring about a condition of gynomonoecism or andromonoecism without necessitating the degeneration of parts. Thus, also, among dioecious forms the appearance of male flowers on the pistillate plants or of female flowers on the staminate plants gives all possible sex combinations found in plants.

There is still another form in which a so-called polygamous condition may exist. In these cases either the female or male elements, although morphologically perfect, are physiologically, either one or both, functionless. We find also gradations in the degree of sterility of stamens or ovaries of parts of the plant, of the whole plant, or of varying numbers of individuals in a group of plants.

Earlier investigators who have observed pistillody of the stamens, staminody of the pistils, the appearance of male flowers on female plants, etc., considered them monstrosities and grouped them as such. Moquin-Tandon (1841) and Masters (1869) include all such phenomena under teratology. The many cases of this sort reported for plants would suggest that this treatment is by no means adequate.

Wehrli (1892), who reports on a case of the complete transformation of a male catkin of *Coryllus avellana* L., has brought together all the available literature from 1741 to 1892. He lists over 80 distinct species, monoecious, dioecious, and hermaphroditic, in which such modifications of floral parts have occurred. The phenomena he observed include: the appearance of

male flowers on female plants, of pistils and stamens in the same catkins, appearance of perfect flowers on male plants, abortion of stamens, pistillody of stamens, staminody of pistils, yearly changes in flowers on a tree (nutmeg), sectorial arrangement of male and female inflorescences in *Pinus alba*, and many more. Wehrli's references and *résumé* are so complete that they have not been repeated here. However, a number of typical examples will be listed from the literature since Wehrli's paper.

Haring (1894) gives an elaborate series of drawings showing various gradations in the transition stages of stamens into pistils and of pistils into stamens in *Salix caprea* L. and *S. cinerea* L. He observes that his work shows the tendency in willows to the greatest plasticity in the structure, form, and sex of the floral organs, including the growing together or the separation of parts, the replacement of one sex organ by that of the opposite sex, and the transition of one sex into the other. The author goes on to say that the phenomena that he has described show the morphological equivalence of the organs of both sexes, in the position of the sex organs no matter whether male or female, in the replacement of the organs of one sex by those of the other, and in the transition of one sex into the other.

In the plant kingdom not only is there a transformation of one sex organ into the opposite but the transmuted organs are quite regularly functional, though sterility of the intergrade organs is not uncommon. Intergradation of sex in plants, if measured in percentages, may be from a fraction of one percent to one hundred percent, in the former case by the pistillody of a single stamen or staminody of a single pistil on a whole plant and in the latter case through the complete alteration of a male plant into a female. Sex intergradation as evidenced by the appearance of one or more parts of the opposite sex on a given plant does not seem to affect the fertility of the plant.

We may note in more detail some of the most carefully studied forms which show these sex intergrades. *Satureja hortensis* is described by Correns (1904) as occurring in three forms: (1) plants with female flowers; (2) plants with hermaphroditic flowers, hermaphroditic flowers with shriveled anthers, and female flowers; (3) plants with hermaphroditic flowers and shriveled anthers, and female flowers. These shriveled anthers indicate a tendency to abortion or infertility of the organs of one or the other sex, paralleling the conditions in Goldschmidt's sex intergrades.

Dimorphotheca pluvialis is trimorphic (Correns, 1913). In an earlier paper (1906) he describes the ray flowers as female, the outer disc flowers as hermaphroditic, and the innermost as male.

Correns (1904) finds five forms of *Silene inflata*: males, females, hermaphrodites, gynomonoecious, and gynodioecious individuals.

Wittrock (1886) describes five different kinds of inflorescences in *Acer platanoides*: (1) individuals exclusively female, (2) individuals whose first flowers are female and their later flowers male, (3) individuals whose first

flowers are male and their later flowers in part male and in part female, (4) individuals whose first flowers are male and their later flowers female, (5) individuals exclusively male.

Schulz (1892), on the basis of eleven years' observation of the ash (*Fraxinus*), recognizes ten distinct forms:

- (1) Individuals which bear only male flowers.
- (2) Individuals which bear only hermaphroditic flowers.
- (3) Individuals which bear only female flowers.
- (4) Individuals which bear only male flowers one year and the next year show branches of both male and female flowers.
- (5) Males which have certain branches either female, hermaphroditic, or with both kinds of inflorescences.
- (6) Individuals which one year bear only female flowers, and the next year have branches with more or less hermaphroditic and female flowers.
- (7) Individuals bearing equal numbers of female and hermaphroditic flowers on the same or different branches.
- (8) Individuals which bear one year only hermaphroditic flowers and almost always associated with them female flowers, later producing male flowers.
- (9) Female or hermaphroditic individuals with male branches.
- (10) Individuals with about equal numbers of male, hermaphroditic, and female flowers.

Correns (1908) says that there are at least thirty intergrading categories recognizable in *Plantago lanceolata*. In his classification of forms for experimental purposes he recognizes the following classes: (1) hermaphrodites, (2) predominantly hermaphrodites, (3) hermaphrodites and females, (4) predominantly females, and (5) females.

I have given only a few examples of the very many that are listed in the plant kingdom, but the forms cited are sufficient to show the wide range of intersexuality that exists among plants. These cases of intergrades in functional and structural development of the sex organs, taken in connection with the classes based on the distribution of the sex organs by plants as individuals as tabulated above, present an almost bewildering completeness as a picture of the theoretically possible gradations in sex characters both of the gametes and of the organisms which produce them. And it is to be remembered that for the most part these are not exceptional or chance cases. They represent the common and obvious facts as to sex in the flowering plants. No theory of sex based on the assumption of the alternative inheritance of fixed sex factors which are segregated at the time of the reduction divisions can do justice to the conditions presented in the higher plants.

I have brought together data as to the distribution of sex forms in the various orders of seed plants. For this purpose I have followed Engler and Gilg's "Syllabus der Pflanzenfamilien." Practically every order has fami-

lies which contain forms that show more than one kind of distribution of the sex elements. Thus in the monocotyledons ten of the eleven orders have hermaphroditic, monoecious, dioecious, and polygamous individuals. There are twenty-two families represented in the ten orders. In the dicotyledons thirty-one of the forty orders have representatives of two or more of the various distributions of the sex elements. There are ninety families that exhibit this tendency. At the end of the paper are listed the families and the sex forms found in each. Their distribution is further shown by means of a table.

CHANGE OF SEX APPARENTLY AS A RESULT OF ENVIRONMENTAL INFLUENCES

Changes of sex from year to year and apparently as a result of environmental influences are inextricably interrelated with the fluctuations of maleness and femaleness in sex intergrades and must hence be briefly considered here.

Gallardo (1901) reports on the work of Spegazzini, who by transplanting wild female plants of *Dioscorea*, *Clematis*, and *Trianosperma* found that the following year fruit was set. Examination showed that these plants bore either male or hermaphroditic flowers besides the female flowers. The following year, however, they became female again. Male plants, transplanted, showed no change of sex.

De Vries (1903) figures the appearance of seeds on a male branch of *Mercurialis annua*. Strasburger (1910) cut back 200 male plants to ascertain whether severe pruning would have any effect upon them. Only one male plant that had been cut back produced a single female flower. One of his plants, no. 16, started as a pure female. It began, however, gradually to develop male flowers with functional pollen. It became more and more male, producing the characteristic odor of the male plants. He collected 55 seeds from this plant but only 5 germinated, 2 males and 3 females being produced. This behavior of Strasburger's plant, with reference to the production of a mixed progeny, might perhaps be explained on the basis that the seeds set when the plant was predominantly female produced female offspring, while the seed produced when the plant was predominantly male produced males. The 55 seeds may even have represented the three conditions, male, female, and hermaphroditic.

Higgins (1916) reports a case in which a male plant of *Carica papaya* was cut down, leaving only a stump. This stump sent out branches which bore abundant fruit.

Pritchard (1916) found that by mutilating male and female plants of hemp the appearance of organs of the opposite sex could be induced. The author calls attention to the presence of monoecious individuals as a normal occurrence, often constituting as high as eight percent of the dioecious cultures.

Davey and Gibson (1917) have found in *Myrica*, which is described as

dioecious, gradations in sex like those described for other forms. They find a small proportion of monoecious plants which represent all gradations between the normal pistillate and staminate types. They also describe bushes and shoots whose sex may vary from year to year. Fourteen cases found to be entirely pistillate in 1913 and 1914 produced staminate catkins in 1915. One plant produced almost entirely staminate catkins. Certain trees and branches which produced abundant fruit in 1913 developed mixed shoots in 1914 and in 1915 became almost staminate.

The classic case of alteration of sex in plants is that of *Lychnis dioica* when attacked by the anther smut fungus, *Ustilago violacea*. Strasburger (1900) points out that both male and female plants are attacked by the smut. In the anthers of the male the parasite causes a characteristic purplish color, the interior of the anther being filled with smut spores. In the female the fungus causes a more profound change. The plant is stimulated to produce anthers with the characteristic sporogenous tissue which tissue is later destroyed by the fungus so that the anther is ultimately filled with fungus spores.

Although the list which I have brought together is by no means complete, it is, however, sufficiently representative of the changes in sex that have been reported in the literature. Sex intergrades, it will be noted, may occur in various degrees, from the transition of one sex organ into that of the opposite sex to a complete change of sex of the entire plant.

SECONDARY SEX CHARACTERS

It is to be noted that intersexualism in animals is measured by the degree of modification of one or the other of the secondary sex characters, by the appearance of secondary sex characters of one sex in individuals of the opposite sex, as well as by the degeneration of ovary or testis or the transition of an ovary into a testis or of a testis into an ovary. In animals sex dimorphism is the characteristic thing, and one is familiar with such differences in sex as size, voice, stature, plumage, and the like.

Sex dimorphism in flowering plants, where the sexes are separate, is not very striking; secondary sex characters have been contrasted but little in such forms. Darwin (1889, page 11) cites the case of the Resteeae of Australia and the Cape of Good Hope, forms which show extreme sex dimorphism. It is reported that often it is impossible to match the male with the female of the same species. Shull (1914) reports for *Lychnis dioica* L. a sex-limited character in the form of narrowness of leaf in the male of *Lychnis dioica angustifolia*. Cook (1914) reports on a case of sex inequality in hemp, where the male plants are smaller and shorter than the females. These male plants die much sooner than the females.

The female inflorescences of *Mercurialis* are borne in clusters in the axils of the leaves, while the male inflorescences are borne in interrupted spikes which surpass the leaves. This characteristic appearance of the

inflorescences of the two sexes may be considered as the secondary sex character of the two sexes, in the sense that the manner in which the inflorescences are borne is characteristic for each sex. No doubt a closer examination of other dioecious forms will show differences in male and female pedicels, petals, and sepals, either by their presence or by their absence.

It is interesting to note that in sex intergradation in *Mercurialis annua* there is no transition of a secondary sex character of one sex into that of the other. Those females which tended towards maleness by producing many male flowers and many seeds did not take on the general growth characteristics of the male. The same holds true for the males that tended towards femaleness—they too still maintained their characteristic form of growth.

THE DOCTRINE OF VARYING POTENCIES IN GERM CELLS

Alternative inheritance of sex is the extreme of a series of intergraded variations. Hermaphrodites (with perfect flowers) and monoecious forms become dioecious not by the sudden development of heterozygosis in one sex and the separation of sex factors in the reduction division, but by the gradual development of sex purity (dioecism) through a long series of intergraded sex variants. The connecting links can all be found in the polygamous (mixed) species. If dioecism has arisen in this way, it is hardly likely that there is anything of the nature of fixed, invariable sex factors in the germ plasm. It is a matter of fluctuating tendencies. Male tends to produce male, female to produce female; sometimes one tendency is stronger, sometimes the other.

Strasburger (1910) attacks Correns' view that one sex is heterozygous for a sex determiner on phylogenetic grounds. The evolutionary trend has been to make the egg and sperm different. Phylogeny points to the egg's being female-producing and the male gamete's being male-producing. It is certainly an awkward assumption that one half the male gametes, for example, must carry female determiners. In an earlier work Strasburger (1909a) concluded that the egg of the dioecious phanerogam tends to produce females only, while in the production of the microspores of a tetrad by division of the pollen mother cell two of the spores will have a stronger male tendency than the other two. Those with the stronger male tendency (which is transmitted to their descendants, the male gametes) will dominate over the female tendency of the egg and thus males will be produced, while the weaker male tendency of the other two will be dominated by the stronger female tendency of the egg and females will result. Noll (1907), from his studies of dioecious plants, was led to this view that there are pollen grains of two strengths as regards the male-producing tendency.

While Strasburger's view explains the behavior of his selfed females and of his selfed males, and the sex of the progeny resulting from the fertilization of a female by a male, there is one difficulty that he overlooked. Assuming that the eggs are all of one kind, then the eggs produced on the

male plants must all dominate over the weaker male gametes. Such however, is not the case. In the female that produces sporadic male flowers there is no reason, on Strasburger's assumption, why the male gametes should not be of two kinds. Selfed females produce only female offspring. That means that the male-producing tendencies transmitted by all the pollen grains of the tetrad are dominated by the female-producing tendency of the egg. On Strasburger's assumption there must now be at least three strengths of pollen grains, if not four: two kinds produced by the male, one of which is subordinate in its sex-determining tendency to the egg, and two kinds (on *a priori* grounds) produced by the sporadic male flowers on the female. Then, too, there are two kinds of eggs instead of one kind: the egg of the female plant which dominates over the weaker male-producing tendency of the pollen grains, and the egg produced upon the male plants, which is dominated by the male-producing tendencies of both kinds of pollen grains, and is thus weaker than the eggs borne on the female plant.

We reach here a conception, which the thus-far meager data on inheritance in dioecious and polygamo-dioecious forms seem to bear out, namely, that *there may be graded potencies in both the gametes, the egg as well as the male gamete, of such forms*. The work of Correns is especially significant. In his work on *Satureja*, *Silene*, and *Plantago* he brings out clearly that the more pronounced the sex of the individual the more marked will be its influence on the sex of its offspring. The normal appearance of sex intergrades (there are at least thirty degrees in *Plantago lanceolata* between pure female and hermaphrodite) is evidence in that direction. The behavior of the females of *Mercurialis* in my cultures is interesting in this respect. The original mother plant produced 66 seeds and 50 offspring. The offspring in turn produced seeds varying in number from 1 to 238. The original mother plant produced eggs of varying potencies as evidenced by the variation in male flower and seed production of the offspring. It is quite natural that the eggs should have varied in their ability to transmit the seed-producing qualities of the mother as in other qualities. Although the offspring tended to be like the mother in the sense that they were pure females or predominantly females, they varied in their ability to produce male flowers and hence seeds. The fertilized egg that produced a female that during its life history produced no male flowers or seeds is different, whether it be qualitatively or quantitatively, from the fertilized egg that produced a plant that produced many male flowers and seeds. One can conceive gradations in the power to produce male flowers and seeds, beginning with eggs with zero potentiality and running thence all the way to those with the potentiality of plant no. VII (Yampolsky, 1919), which produced 32 male flowers and 230 seeds.

The male cultures of *Mercurialis annua*, while they do not show the tendency toward intergradations as often as do the females, nevertheless bring out very clearly gradations in sex potency.

On the assumption that gametes vary or are graded in strength, the one-to-one ratio may be explained in dioecious forms, especially in dealing with mass populations. As has already been pointed out (*l.c.*), it is only when large numbers are considered that the one-to-one ratio appears. To be sure the law of chance comes into effect in such an explanation of sex ratios. The explanation of the one-to-one ratio may very well lie in the assumption that the gametes of the female have as much chance to dominate over the male gametes as the male gametes have to dominate over the female. That the gametes of one sex may in cases completely or almost completely dominate over those of the other sex is brought out in aberrant sex ratios. This advantage may, when large numbers of individuals are considered, be offset by a parallel condition resulting in the dominance of gametes of the other sex (Doncaster, 1913, 1916; Montgomery, 1908).

In *Mercurialis*, though the species is prevailingly dioecious, it is obvious that we must assume that the potentialities for the development of both sexes are present in practically all the individuals of the species. There is nowhere evidence that sex is determined in this plant by the presence or absence of a sex-determining factor. Those individuals which remain purely male or purely female throughout are not to be conceived as very different from those which produce a few flowers of the opposite sex. There is no evidence for the localization of the sex difference either in a special part of the plant or in a special part of the cell. The appearance of the sporadic flowers of the other sex may occur anywhere on the plant and at any stage of its development. Their occurrence is comparable to that of bud variation, and like the latter they show that the organism may contain latent potentialities as well as visibly expressed characters. Nor does the production of a few flowers of the other sex alter essentially the sex character of the plant as a whole. It is still prevailingly male or female and transmits its sex as such. It is highly probable that as a rule at least the pollen from sporadic male flowers on a female plant pollinates the nearest female flowers on the same branch. The seeds so produced, however, grow into female plants like the branch which bore them. It is sometimes questioned whether a plant with its potentialities of unlimited growth and with its successive crops of reproductive organs is an individual in the sense that an animal is, with its more limited growth and definitely localized reproductive and other organs. The behavior of these prevailingly dioecious *Mercurialis* plants with reference to sex transmission certainly shows that they are unit individuals male or female in a very strict sense. But it is just as clear that, as noted above, the dioecious condition is only an extreme, a climax condition in the evolution of sex differentiation. As the data at the end of this paper show, the transition from the hermaphroditic and monoecious to the polygamo-dioecious and dioecious condition is going on at numerous and widely distributed points in the orders and families of seed plants.

DISTRIBUTION OF SEX FORMS ACCORDING TO ENGLER AND GILG

Monocotyledons

Order Pandanales

Pandanaceae: monoecious, dioecious, polygamo-dioecious

Order Helobiae

Potamogetonaceae: monoecious, dioecious, hermaphroditic

Naiadaceae: monoecious, dioecious, hermaphroditic

Scheuchzeriaceae: monoecious, dioecious, hermaphroditic

Alismataceae: monoecious, dioecious, hermaphroditic

Hydrocharitaceae: monoecious, dioecious, hermaphroditic

Order Triuridales

Triuridaceae: monoecious, dioecious, hermaphroditic

Order Glumiflorae

Gramineae: monoecious, dioecious, hermaphroditic

Cyperaceae: monoecious, dioecious, hermaphroditic

Order Principes

Palmae: monoecious, dioecious, hermaphroditic

Order Spathiflorae

Araceae: Monoecious, dioecious, hermaphroditic

Order Farinosae

Flagellariaceae: monoecious, hermaphroditic

Restionaceae: dioecious, hermaphroditic

Centrolepidaceae: monoecious, hermaphroditic

Eriocaulaceae: monoecious, dioecious, polygamous

Commelinaceae: monoecious, hermaphroditic

Order Liliiflorae

Liliaceae: mostly hermaphroditic, dioecious (Smilax, Britton)

Dioscoreaceae: monoecious, dioecious, hermaphroditic

Order Scitamineae

Musaceae: monoecious, hermaphroditic

Zingiberaceae: monoecious, hermaphroditic

Marantaceae: monoecious, hermaphroditic

Order Microspermae

Orchidaceae: mostly hermaphroditic

(Cataseteae): hermaphroditic, monoecious

Dicotyledons

Order Piperales

Piperaceae: monoecious, hermaphroditic

Chloranthaceae: monoecious, hermaphroditic

Order Salicales

Salicaceae: monoecious, dioecious

Order Myricales

Myricaceae: monoecious, dioecious

Order Balanopsidales

Balanopsidaceae: dioecious

Order Leitneriales

Leitneriaceae: dioecious

Order Batidales

Batidaceae: dioecious

Order Julianiales

Julianiaceae: dioecious

Order Fagales

Betulaceae: monoecious, rarely dioecious

Fagaceae: monoecious, rarely hermaphroditic

Order Urticales

Ulmaceae: monoecious, dioecious, polygamous, hermaphroditic

Moraceae: monoecious, dioecious

Urticaceae: monoecious, dioecious, polygamous, hermaphroditic

Order Proteales

Proteaceae: monoecious, hermaphroditic

Order Santalales

Santalaceae: monoecious, dioecious, hermaphroditic

Loranthaceae: monoecious, dioecious, hermaphroditic

Order Aristolochiales

Rafflesiaceae: monoecious, hermaphroditic

Order Polygonales

Polygonaceae: monoecious, dioecious, polygamous, hermaphroditic

Order Centrospermae

Chenopodiaceae: monoecious, dioecious, hermaphroditic

Amarantaceae: rarely monoecious, dioecious, polygamous, hermaphroditic

Nyctaginaceae: monoecious, hermaphroditic

Phytolaccaceae: monoecious, polygamous, hermaphroditic

Caryophyllaceae: monoecious, dioecious

Order Ranales

Ceratophyllaceae: monoecious, dioecious

Trochodendraceae: monoecious, hermaphroditic

Cercidiphyllaceae: dioecious

Ranunculaceae: dioecious, hermaphroditic

Lardizabalaceae: monoecious, hermaphroditic

Menispermaceae: dioecious

Magnoliaceae: monoecious, hermaphroditic

Monimiaceae: monoecious, hermaphroditic

Lauraceae: monoecious, dioecious, polygamous, hermaphroditic

Hernandiaceae: monoecious, hermaphroditic

Order Rosales

Hydrostachyaceae: dioecious

Saxifragaceae: polygamo-dioecious, hermaphroditic

Hamamelidaceae: monoecious, polygamous, hermaphroditic

Rosaceae: polygamo-dioecious, hermaphroditic

Connaraceae: monoecious, hermaphroditic

Leguminosae: monoecious, dioecious, polygamo-dioecious, hermaphroditic

Order Pandales

Pandaceae: dioecious

Order Geraniales

Rutaceae: polygamo-dioecious, hermaphroditic

Simarubaceae: polygamous, dioecious, hermaphroditic

Burseraceae: dioecious, hermaphroditic

Dichapetalaceae: dioecious, hermaphroditic

Euphorbiaceae: monoecious, dioecious

Callitrichaceae: monoecious, hermaphroditic

Order Sapindales

Buxaceae: monoecious, dioecious

Empetraceae: monoecious, dioecious, polygamous

Coriariaceae: monoecious, hermaphroditic

- Anacardiaceae: polygamo-dioecious, hermaphroditic
- Aquifoliaceae: dioecious, polygamo-dioecious
- Salvadoraceae: dioecious, hermaphroditic
- Icacinaceae: monoecious, hermaphroditic
- Aceraceae: dioecious, polygamous
- Hippocastanaceae: polygamous
- Sapindaceae: polygamo-dioecious
- Sabiaceae: polygamo-dioecious, hermaphroditic
- Order Rhamnales
 - Rhamnaceae: polygamous, hermaphroditic
 - Vitaceae: polygamo-dioecious, hermaphroditic
- Order Malvales
 - Sterculariaceae: monoecious, hermaphroditic
- Order Parietales
 - Dilleniaceae: monoecious, hermaphroditic
 - Guttiferae: monoecious, hermaphroditic
 - Calophylloideae: monoecious, hermaphroditic
 - Flacourtiaceae: monoecious, dioecious, hermaphroditic
 - Stachyuraceae: polygamous, hermaphroditic
 - Passifloraceae: monoecious, hermaphroditic
 - Datiscaceae: monoecious, dioecious, hermaphroditic
- Order Myrtiliflorae
 - Elaeagnaceae: monoecious, dioecious, polygamous, hermaphroditic
 - Sonneratiaceae: monoecious, hermaphroditic
 - Nyssaceae: monoecious, hermaphroditic
 - Combretaceae: monoecious, hermaphroditic
 - Halorrhagaceae: monoecious, dioecious, hermaphroditic
 - Cynomoriaceae: monoecious, hermaphroditic
- Order Umbelliflorae
 - Araliaceae: monoecious, polygamous, hermaphroditic
 - Umbelliferae: monoecious, polygamous, hermaphroditic
 - Cornaceae: monoecious, hermaphroditic
- Order Primulales
 - Theophrastaceae: monoecious, hermaphroditic
 - Mrysinaceae: monoecious, hermaphroditic
- Order Ebenales
 - Ebenaceae: dioecious, polygamous, hermaphroditic
 - Styracaceae: hermaphroditic, rarely polygamo-dioecious (Britton)
- Order Contortae
 - Oleaceae: monoecious, dioecious, hermaphroditic
 - Loganiaceae: monoecious, hermaphroditic
 - Gentianaceae: monoecious, hermaphroditic
- Order Plantaginales
 - Plantaginaceae: monoecious, hermaphroditic
- Order Rubiales
 - Rubiaceae: rarely monoecious, hermaphroditic
 - Valerianaceae: monoecious, dioecious, polygamo-dioecious, **hermaphroditic**
- Order Cucurbitales
 - Cucurbitaceae: monoecious, dioecious, hermaphroditic
- Order Campanulatae
 - Stylidiaceae: monoecious, hermaphroditic
 - Calyceraceae: monoecious, hermaphroditic
 - Compositae: monoecious, dioecious, polygamous, hermaphroditic

NUMBERS OF FAMILIES IN DIFFERENT ORDERS SHOWING THE VARIOUS
TYPES OF SEX ARRANGEMENT.

Type I.. Dioecious.

Type II. Dioecious, monoecious.

Type III. Dioecious, monoecious, hermaphroditic.

Type IV. Dioecious, hermaphroditic.

Type V. Dioecious, polygamous.

Type VI. Dioecious, polygamous, hermaphroditic.

Type VII. Dioecious, polygamous, monoecious.

Type VIII. Dioecious, polygamous, monoecious, hermaphroditic.

Type IX. Polygamous.

Type X. Polygamous, hermaphroditic.

Type XI. Polygamous, hermaphroditic, monoecious.

Type XII. Monoecious, hermaphroditic.

Order	Types											
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
Pandanales.....							I					
Helobiae.....			5									
Triuridales.....			I									
Glumiflorae.....			2									
Principes.....			I									
Spathiflorae.....			I									
Farinosae.....				I			I					3
Liliiflorae.....			I	I								
Scitamineae.....												3
Microspermae.....												I
Piperales.....												2
Salicales.....		I										
Myricales.....		I										
Balanopsidales.....	I											
Leitneriales.....	I											
Batidales.....	I											
Julianiales.....	I											
Fagales.....		I										I
Urticales.....	—	I	—	—	—	—	—	2				
Proteales.....												I
Santalales.....	—	—	2									
Aristolochiales.....												I
Polygonales.....								I				
Centrospermae.....	—	I	I				I	I	—	—	I	I
Ranales.....	2	I	—	I				I				5
Rosales.....	I							I	—	2	I	I
Pandales.....	I											
Geraniales.....	—	I	—	2	—	I				I		I
Sapindales.....	—	I	—	I	2	—	I		2	2		2
Rhamnales.....										2		
Malvales.....												I
Parietales.....			2									4
Myrtiflorae.....			I					I		I		4
Umbelliflorae.....			3									I
Primulales.....												2
Ebenales.....						I				I		
Contortae.....			I									2
Plantaginales.....												I
Rubiales.....								I				I
Cucurbitales.....			I									
Campanulatae.....								I				2
Total—Families.....	8	8	22	6	2	2	4	9	2	9	2	40
—Orders.....	7	8	13	5	I	2	4	8	I	6	2	21

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